

Diving behaviour and foraging location of female southern elephant seals from Patagonia

C. CAMPAGNA^{1,2},

¹*Centro Nacional Patagónico, CONICET, 9120 Puerto Madryn, Chubut, Argentina*

²*NYZS The Wildlife Conservation Society, New York, NY 10460, USA*

B. J. LE BOEUF, S. B. BLACKWELL, D. E. CROCKER AND F. QUINTANA¹

Institute for Marine Sciences and Department of Biology, University of California, Santa Cruz, CA 95064, USA

(Accepted 16 June 1994)

(With 6 figures in the text)

Our aim was to describe the free-ranging diving pattern and to determine the location of foraging of pregnant female southern elephant seals, *Mirounga leonina*, from Peninsula Valdés, Argentina. This colony is unusual in two respects: it is removed from deep water by a broad shallow shelf (345–630 km wide), and colony numbers have been increasing in recent years in contrast to numbers from other southern hemisphere colonies that are stable or in decline. Microprocessor controlled, geolocation-time-depth recorders were deployed on four females, recording a total of 15,836 dives (270 dive days) during the period February to April, 1992. Departing seals crossed the continental shelf quickly (54.5–62.1 h) and did not show signs of foraging until reaching deep water, due east of the colony in the South Atlantic Ocean. Diving was virtually continuous (93% of the time underwater) with overall mean (\pm S.D.) rates of 2.5 ± 0.2 dives/h, mean dive durations of 22.8 ± 7.1 min (maximum dive duration = 79 min) with 1.6 ± 0.6 min surface intervals between dives, and dive depths of 431 ± 193 m (maximum dive depth = 1,072 m). The diving pattern of females from Patagonia is similar to that of seals from colonies where numbers are decreasing (Macquarie stock) or are stable (South Georgia Island). Our subjects did not, however, feed in or south of the Antarctic Polar Front, or in cold waters along the Antarctic coast, where seals from declining or stable colonies forage.

Contents

	Page
Introduction	56
Background information	57
Methods	57
Subjects	57
Instrument attachment and recovery	57
Diving instruments	58
Estimating migratory paths and foraging location	58
Dive types	58
Results	59
Database	59
Summary dive statistics and diving pattern	59
Behaviour over the continental shelf	62
Location and diving–foraging pattern beyond the continental shelf	64

Discussion	64
Absence of foraging on the continental shelf	68
Foraging location	68
The diving pattern of Patagonian elephant seals compared to seals from other colonies	69
References	70

Introduction

Southern elephant seals, *Mirounga leonina*, whose breeding range is circumpolar in Antarctic and sub-Antarctic waters (Laws, 1994), have decreased significantly in number during the last half of this century (Skinner & van Aarde, 1983; McCann, 1985; Burton, 1986; Hindell & Burton, 1987; Hindell, 1991; Laws, 1994). The percentage decline in census counts over the last 40 years, for colonies in the Southern Ocean adjacent to the Antarctic Polar Front, is estimated at 50% for Heard Island, 84% for Marion Island, 57% for Macquarie Island, 90% for Campbell and Signy Islands, and up to 80% for some colonies in the Kerguelen archipelago (Laws, 1994). The South Georgia colony, with more than 350,000 seals, is considered to have remained stable since the 1950s, but this estimate is based on only two censuses (Laws, 1960; McCann, 1985).

The cause of the reduction in number of southern elephant seals is unknown but is evidently due to factors operating mainly during the pelagic phase of the annual cycle because increases in mortality during the terrestrial phase are not evident (Laws, 1994; Hindell, Slip & Burton, 1994). Depletion of food resources is suspected to be one of the causes of the decline (Hindell, 1990). The effect is specific to elephant seals since other mammalian populations and avian populations of the Southern Ocean have not evidenced similar declines over the same period (Hindell *et al.*, 1994).

The aim of this study was to examine the at-sea behaviour of pregnant females from Península Valdés, Argentina, the only southern elephant seal colony known to have been increasing in numbers during the last two decades (Campagna & Lewis, 1992; Le Boeuf & Laws, 1994). This Patagonian colony is the most northerly large colony (10,000 pups produced in 1992) and it is located in temperate rather than sub-Antarctic waters (Campagna & Lewis, 1992; Campagna, Lewis & Baldi, 1993). Pup production increased 150% from 1975 to 1992 (Vergani, Lewis & Stanganelli, 1987; Campagna & Lewis, 1992; Campagna & Lewis, unpubl. data). By comparing the location and diving–foraging pattern of seals from Patagonia with those of colonies that are in decline (Macquarie and Marion Islands) or stable (South Georgia), we hoped to elucidate factors responsible for fluctuations in colony number throughout the breeding range. The location of diving reflects the sites of foraging because all foraging occurs during diving. Location and the pattern of diving reflects the general type of prey consumed (e.g. pelagic or benthic animals), the periodicity of foraging, and the effort expended (Le Boeuf *et al.*, 1993; Le Boeuf & Laws, 1994).

We studied the at-sea behaviour of pregnant females, reasoning that successful foraging during gestation is positively correlated with pup production, which is vital for population growth. We recorded the first 2½ months of pregnancy; instrument limitations prevented the recording of the entire eight months at sea, the full gestation period. We sought to determine the migratory paths, the location of foraging and the free-ranging dive pattern throughout the period at sea. We examined diving on and off the continental shelf because the shelf is unusually broad (345 to 630 km between 40 and 48° S), shallow (<200 m), and supports a rich commercial fishery for squid, *Illex argentinus* and *Loligo* spp., and hake, *Merluccius hubbsi* (Bellisio, López & Torno,

1979; Csirke, 1987; Podestá, 1990), known prey of elephant seals (Laws, 1956, 1977; Clarke & MacLeod, 1982; Rodhouse *et al.*, 1992; see also Antonelis *et al.*, 1994 regarding the northern hemisphere congener, *M. angustirostris*). We tested the hypothesis that Patagonian seals may be thriving, relative to seals from other colonies, because they exploit prey on the shallow continental shelf rather than migrating far and diving deeply. Lastly, we attempt to explain fluctuations in colony growth by comparing the diving and foraging behaviour of the Patagonian seals with those studied by similar methods at other colonies.

Background information

Southern elephant seals, like northern elephant seals, make biannual, round trip migrations lasting 2–8 months and covering 2,000–7,500 km, during which they dive continuously (Hindell, Burton & Slip, 1991; DeLong, Stewart & Hill, 1992; McConnell, Chambers & Fedak, 1992; Le Boeuf *et al.*, 1993; Stewart & DeLong, 1994; Fedak *et al.*, 1994). Following lactation, females go to sea for approximately two months then return to land to moult, which lasts about one month. The feeding trip to sea following the moult covers the entire period of gestation and lasts eight months, ending with return to the rookery to give birth, lactate and mate (Laws, 1956; McCann, 1985; Campagna *et al.*, 1993; Le Boeuf, 1994). Females of both species dive deeply (modal depths of 300–600 m), for long periods (mean dive durations of 20–22 min) and virtually continuously during the entire period at sea (Le Boeuf *et al.*, 1988, 1989, 1993; Naito *et al.*, 1989; Hindell, 1990; Hindell, Burton & Slip, 1991; McConnell *et al.*, 1992).

Methods

Subjects

Five tagged adult females, of medium size and estimated to be 6 years of age, with a known history of having bred in the area, were selected from 1,500 seals that were moulting near Punta Delgada, Peninsula Valdés, Argentina, during February, 1992. Each female was marked individually and monitored throughout her stay on land.

Instrument attachment and recovery

A geographic-location time-depth-recorder (GLTDR; Wildlife Computers, Woodinville, Washington) and a VHF transmitter (Advanced Telemetry Systems, Bethel, Minnesota) were attached to each female approximately 2 weeks after the completion of the moult at the beginning of gestation, just before they were ready to go to sea.

Females were anaesthetized with an intramuscular injection of 16–19 ml of Ketamine hydrochloride (4–5 mg/kg of 100 mg/ml of Ketaset, Bristol Laboratories, Syracuse, New York; see Briggs, Hendrickson & Le Boeuf, 1975) and 1–2 ml of 5 mg/ml diazepam (Valium, Roche Laboratories, Nutley, New Jersey). Subsequent injections of Ketamine (1–1.5 ml) and diazepam (1–2 ml) were administered intravenously as needed. The pelage was cleaned with acetone and a plastic mould was placed on the dorsal midline above the shoulders (Le Boeuf *et al.*, 1988). The mould was filled with marine epoxy (Evercoat Ten-set, Fibre-Evercoat Co., Cincinnati, Ohio) and the adhesive was worked under the hair. A GLTDR and a radiotransmitter were attached to a wooden plate with hose clamps. The plate was embedded in the epoxy with the package parallel to the long axis of the seal and with the pressure transducer facing the rear of the animal (see Fig. 1 in Le Boeuf *et al.*, 1988). The attachment was firm within 20 min. Each female left the rookery and departed to sea within 5 h of the last drug administration.

The search for returning females at breeding and moulting sites along a 60 km segment of the coastline began in late August and was conducted bi-weekly throughout the breeding season until early November. A scanning VHF radio receiver (Telonics, Mesa, Arizona) was used. An aerial survey of the entire rookery was conducted on October 2.

Diving instruments

Microprocessor controlled GLTDRs were equipped with a pressure transducer, a quartz clock, a temperature probe and a light sensor mounted in a clear plastic cap (DeLong *et al.*, 1992). Each data logger was enclosed in a cylindrical titanium housing 2.9 cm in diameter by 15.4 cm long; the entire unit weighed 196 g.

Instruments were programmed to collect data continuously as soon as the seals entered the water, recording hydrostatic pressure (dive depth) every 30 sec, ambient temperature at 10 min intervals, and ambient light levels at 15 min intervals until the memory capacities of the computers (256 kbytes) were full.

Upon retrieval, the data were transferred to a personal computer. Software by Wildlife Computers provided summary analyses of the diving data. Additional analyses were conducted using the SAS statistical package (SAS Institute, Inc., 1985).

Estimating migratory paths and foraging location

Location during migration was estimated every 2 days from surface light level readings and temperature data (DeLong *et al.*, 1992; Le Boeuf *et al.*, 1993; Hill, 1994). Daily light-level curves were used to estimate time of dawn and dusk from which an algorithm calculated approximate latitudinal and longitudinal position (Hill, 1994). Latitudinal ranges were corrected by matching sea-surface temperature data (SST), recorded when the seal surfaced, to oceanographic data for the South Atlantic Ocean (Gordon & Molinelli, 1992). Latitudinal location error, greatest during the equinoxes, is estimated to be at least 60 km (DeLong *et al.*, 1992; Stewart & DeLong, 1994; S. Blackwell & B. Le Boeuf, unpubl. data). Daily temperature/depth profiles at various times in the migration provided additional general estimates of latitude (Hindell, 1990; Hindell, Burton & Slip, 1991). The minimum round trip migration distance for a seal was calculated by doubling the distance in kilometres along a great circle between Punta Delgada (42.8° lat. S, 63.6° long. W) and the point furthest away on the animal's track.

Dive types

From a strip-chart representation of the time-depth profile of all dives for each female, 2 of us classified each dive into 1 of 4 major types and a miscellaneous category following Le Boeuf *et al.* (1992, 1993). The major dive types distinguished were: A dives—direct descent to a sharp or rounded inflection point, followed by direct ascent to the surface; C dives—direct descent to a depth, at which point the descent rate decreases, then continues at a slower rate to the bottom of the dive, followed by direct ascent to the surface; D dives—rapid descent to variable depths followed by 2–12 vertical excursions reflecting changes in depth at the bottom of the dive, followed by rapid ascent to the surface; E dives—rapid descent to the bottom of the dive, which is uniformly flat, indicating a constant depth at the bottom of the dive, followed by a rapid ascent to the surface. The miscellaneous category, X dives, included dives that were shallow (<25 m) and brief (≤ 1 min), most of which occurred during departure from the rookery over the continental shelf.

Based on several criteria (e.g. location of diving in relation to depth of ocean bottom, swim speed, dive shape and horizontal distance covered), Le Boeuf *et al.* (1992, 1993) concluded that A dives serve transit, C dives serve a physiological process such as digestion, sleep or rest, D dives serve pelagic foraging, and E dives serve foraging near the continental slope, especially by males. Transit and foraging dives of both types are the same as those identified by Hindell, Burton & Slip (1991) as Types 4, 1 and 2, respectively.

Results

Database

We recovered four of the five instruments; they recorded a total of 15,836 dives during 271 dive-days. This encompassed the first 2½ months at sea for each female or the first trimester of pregnancy. The light-level sensor of female 2 failed but the other three GLTDRs provided geolocation data for 64 to 70 days.

Summary dive statistics and diving pattern

All females exhibited a general diving pattern similar to those described for female southern and northern elephant seals from other colonies (e.g. Le Boeuf *et al.*, 1988, 1989; Boyd & Arnborn, 1991; Hindell, Slip & Burton, 1991), i.e. virtually continuous diving throughout the period at sea with dives being deep and of long duration followed by brief intervals at the surface (Table I).

Mean dive duration was 22.8 ± 7.1 min (Table I). The modal dive duration was 20 min; 84% of the dives were in the interval 15–30 min (Fig. 1). All females had maximum dives that exceeded 1 h. Each female spent 92–94% of the time at sea underwater.

Mean surface interval between dives (Fig. 1), excluding extended surface intervals (ESIs) longer than 5 min, was 1.6 ± 0.6 min (Table I). ESIs were rare (0.2% of the total surface intervals), ranged in duration from 0.2 to 3.7 h, and occurred only in waters deeper than 200 m. Total ESIs per record ranged from 2–17. One female dived continuously without an ESI for 58 days (3587 dives). Surface interval duration did not vary with the duration of the preceding or succeeding dive. Mean surface interval duration before and after the 10 longest dives (each greater than 60 min) was 1.7 ± 0.6 min and 1.5 ± 0.9 min, not significantly different from the overall mean surface interval shown in Table I ($t = 0.28$, $d.f. = 0, 60$, $P > 0.01$).

Mean dive depth was 431 ± 193 m (Fig. 1) with two females exhibiting maximum dives exceeding 1000 m. Modal dive depth of three females was in the range 450–500 m; the mode of the fourth female was 550–600 m. Dives less than 100 m deep (excluding X type dives) were restricted to the beginning of each record when the seals were on the continental shelf.

TABLE I
Summary statistics from diving records of four female southern elephant seals

Subj.	No. dives	Days at sea	Mean dive/h	Mean depth (m)	Max. depth (m)	Mean dur. (min)	Max. dur. (min)	Mean surf. interval* (min)	Max. surf. interval (min)	Percent time diving
1	3,948	70	2.4	$409 \pm 182^{**}$	971	23.8 ± 8.5	79	1.6 ± 0.6	20	94
2	4,137	68	2.6	402 ± 199	1053	21.7 ± 7.1	64	1.6 ± 0.6	65	93
3	4,080	64	2.7	454 ± 203	1072	20.5 ± 6.0	62	1.7 ± 0.6	222	92
4	3,671	69	2.2	460 ± 188	990	25.2 ± 6.6	62	1.5 ± 0.5	17	93
Total	15,836	271								
Mean	3,959	67.8	2.5	431	1021	22.8	67	1.6	81	93
S.D.	208	2.6	0.2	193	49	7.1	8	0.6	97	1

* Excludes surface intervals over 5 min long

** ± Refers to plus or minus one standard deviation

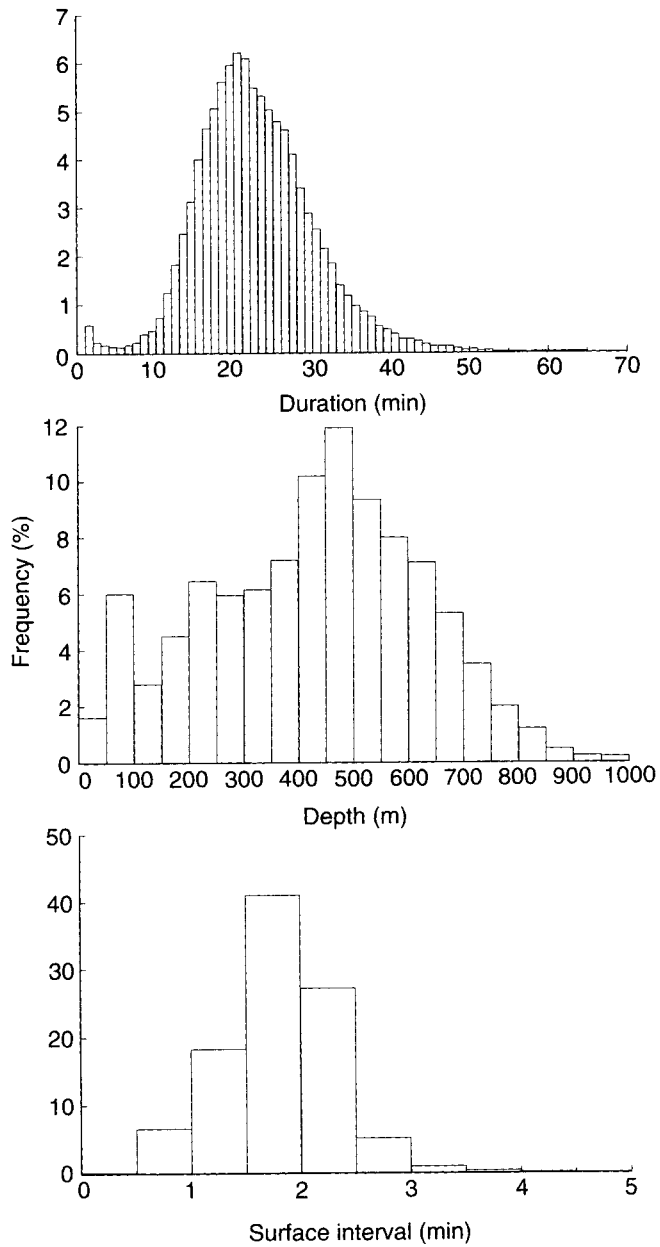


FIG. 1. Frequency distributions of dive duration, dive depth and surface intervals between dives (excluding rare surface intervals greater than 5 min) for four adult females from Patagonia.

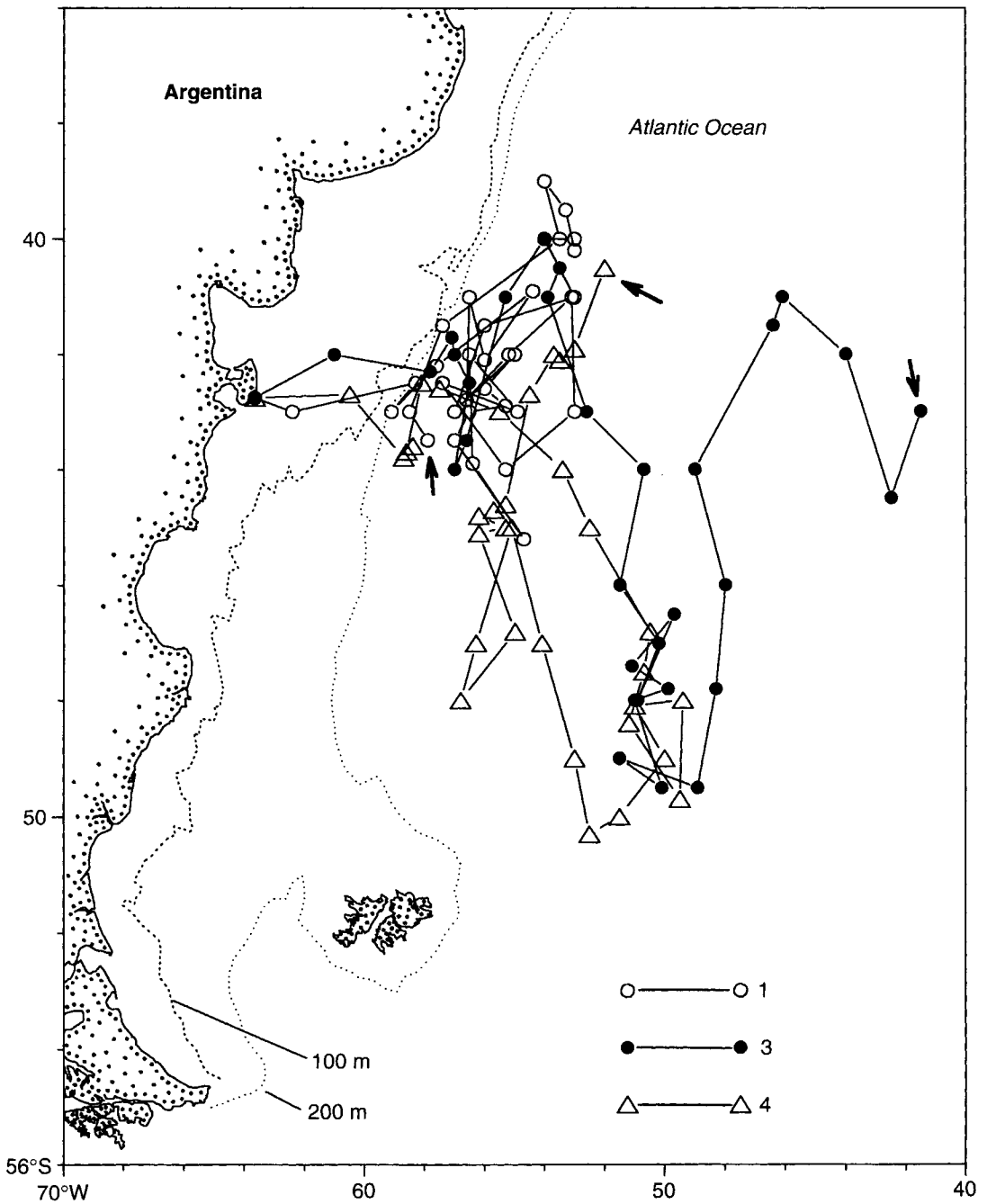


FIG. 2. Migratory paths of three adult females (1, 3 and 4) after moulting at Punta Delgada, Península Valdéz, Argentina. The positions were plotted every two days. Broken lines indicate the 100 and 200 m isobaths. Longitude and latitude are represented on the x and y-axes, respectively. The arrows denote the last position recorded.

Behaviour over the continental shelf

The route, speed and diving pattern on leaving the rookery provide strong indirect evidence that little, if any, foraging occurred on the continental shelf. All females proceeded directly eastward across the continental shelf to deep water (Fig. 2), and spent only 3.7% of their dive record duration, on average, on the shelf.

Females crossed the continental shelf in less than $2\frac{1}{2}$ days, all of them reaching deep water (>200 m) in a similar amount of time and a similar number of dives (Table II). This uniform performance and the tracks of three females (Fig. 2), suggest that all females took a similar eastward route across the shelf. The distance to the 200 m isobath at this latitude is about 360 km which yields a mean horizontal swim speed of 1.68 ± 0.10 m/s (145 km/day). If females had travelled south-east and taken the shortest route to the shelf edge, a distance of 345 km, their mean horizontal swim speed would have been only slightly slower, 1.61 ± 0.09 m/s (139 km/day). All females had significantly higher diving rates and shorter dive durations on the shelf than off it (paired *t*-tests, *t* = 9.1 and 10.2, respectively, *P* < 0.01; Table II). Surface interval durations were shorter on the shelf than off it, but not significantly so (Table II).

The diving pattern on and off the shelf differed. The majority of the dives on the shelf were either flat-bottomed, substratum-limited E-type dives (26%) or shallow D-type dives containing small up and down excursions ('wiggles') of 5–15 m (39%). Spiked dives, associated with long distance transit in deep water, were relatively infrequent (8%) and C-type dives, hypothesized to be associated with food processing (Le Boeuf *et al.*, 1993), were absent in all records. X dives made up the remaining 28%.

When females reached deep water, their diving pattern changed abruptly, with dives becoming deeper, longer and followed by longer surface intervals (Fig. 3, Table II). The majority of the dives beyond the continental shelf were D-type foraging dives with vertical excursions of 10 to 55 m at the bottom of the dives (Table III). Flat-bottomed, E-type dives were exceedingly rare (only two in all four records). Spiked, A-type, transit dives accounted for almost 15% of the dives. C-type dives accounted for about 8% of the dives.

TABLE II

Diving behaviour of four female southern elephant seals on the continental shelf while leaving the rookery and off the continental shelf in deep water (>200 m). Mean horizontal travel speed on the shelf was calculated using the great circle distance between Punta Delgada and the point due east on the 200 m isobath (about 360 km)

Seal	On the Continental Shelf					Off the Continental Shelf			
	Number of dives	Hrs on shelf	Travel speed (km/h)	Dives per hr	Mean dive dur. (min)	Surface int. (min)	Dives per hr	Mean dive dur. (min)	Surface int. (min)
1	258	54.5	6.6	4.7	$11.3 \pm 4.2^*$	1.1 ± 0.5	2.3	24.7 ± 8.1	1.6 ± 0.7
2	249	60.0	6.0	4.2	12.9 ± 4.6	1.0 ± 0.5	2.5	22.1 ± 7.0	1.7 ± 1.7
3	266	62.1	5.8	4.3	12.1 ± 3.3	1.6 ± 1.2	2.6	21.0 ± 5.8	1.5 ± 0.6
4	231	61.5	5.9	3.8	14.6 ± 3.9	1.1 ± 1.9	2.2	26.0 ± 6.1	1.5 ± 0.6
Sum	1004	238.1							
Mean	251	59.5	6.1	4.2	12.7	1.1	2.4	23.4	1.6
S.D.	15	3.5	0.4	0.4	4.1	0.6	0.2	7.1	0.9

* ± Refers to plus or minus one standard deviation

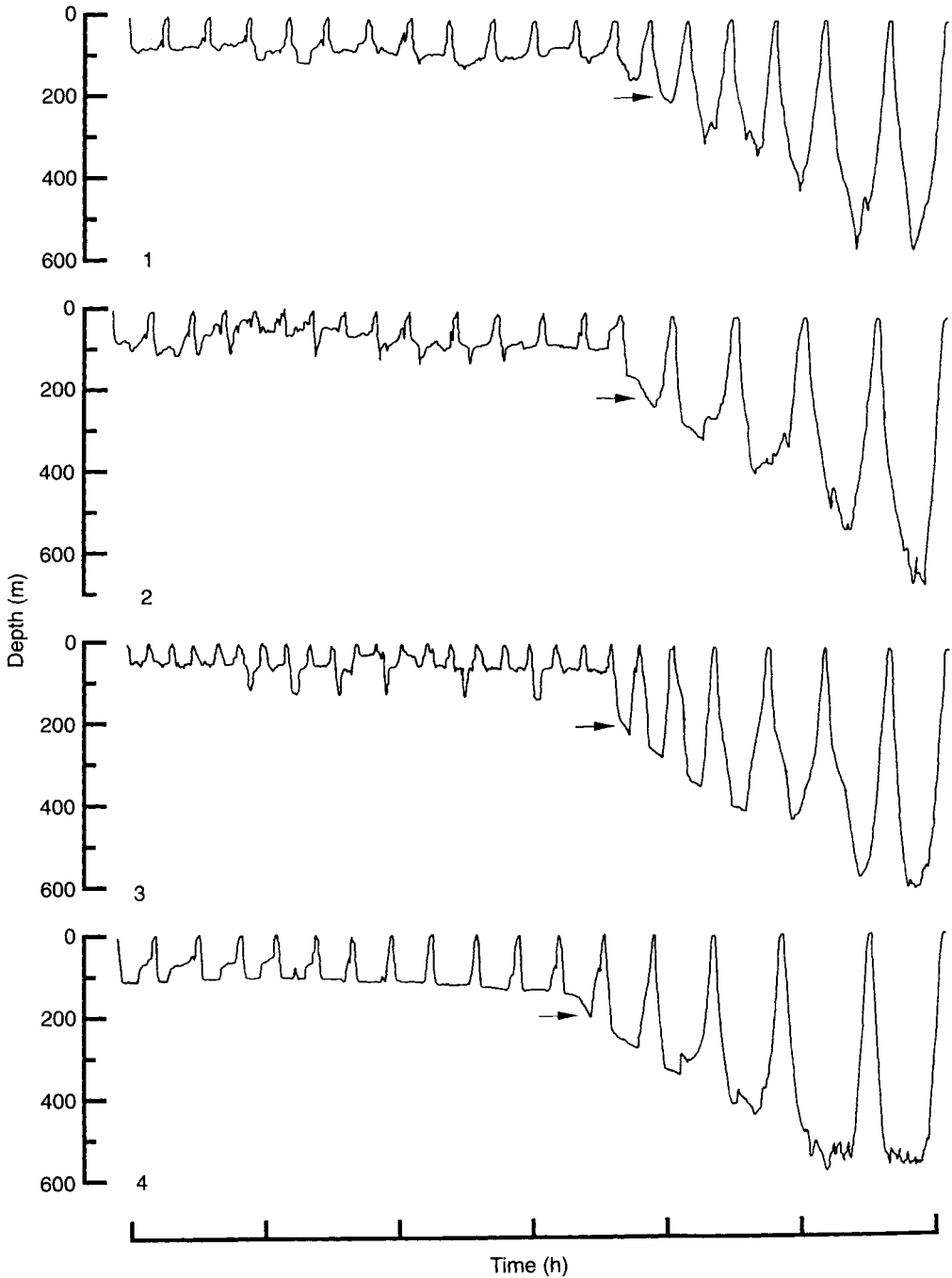


FIG. 3. Excerpts from the diving records of four adult females from Patagonia showing the transition from diving in shallow water over the continental shelf to crossing the 200 m isobath (the arrow indicates the depth) and diving in deep water.

TABLE III

Percentage distribution of dives beyond the continental shelf of four female southern elephant seals into five dive types. Four of the dive types are assumed to serve transit (A), physiological processing (C), pelagic foraging (D), and benthic foraging (E). X dives were brief, shallow and unclassifiable (see text)

Female	Dive types				
	A	C	D	E	X
1	16.5	9.5	70.8	0.1	3.2
2	15.2	7.3	75.0	0.0	2.5
3	14.5	8.3	70.5	0.1	6.5
4	12.4	9.2	72.9	0.0	5.5
Mean	14.7	8.6	72.3	0.1	4.4
S.D.	1.7	1.0	2.1	0.1	1.9

Location and diving-foraging pattern beyond the continental shelf

Geolocation tracks, water temperature/depth profiles and diving patterns support the conclusion that foraging was concentrated in deep, temperate waters of the south Atlantic Ocean east of the rookery. Light level and SST data show that three females spent most of their time over deep water up to 1,800 km east of Península Valdés (45° W) in the latitude range, 39–50° S (Fig. 2). Once deep water was reached, the routes taken by each of the three females were not unidirectional but rather, contained loops and reversals. Minimum round trip migration distances for females 1, 3 and 4 were 1,876, 2,657 and 3,596 km, respectively.

Daily water temperature/depth profiles provide additional evidence that the seals foraged in the area shown in Fig. 2; the profiles are characteristic of those of the south-eastern Atlantic Ocean north of the Antarctic Polar Front (Gordon & Molinelli, 1992). Water temperature decreased rapidly with depth to about 100 m and thereafter remained constant or decreased slowly with further increases in depth. This sharp, shallow thermocline was evident in all records throughout the period at sea over deep water. Mean daily SSTs were in the range 8–16 °C, while water temperature at 100–500 m hovered around 4 °C, occasionally reaching a low of about 2 °C. Water temperature/depth profiles for a day midway in the migration are typical of most of the period at sea (Fig. 4).

The diving pattern suggests that prey were pursued in the deep scattering layer. Over 70% of the dives off the shelf were of the D type, indicative of pelagic foraging. For each female, these dives were deeper during daylight hours than at night (Fig. 5), which accounts for longer dive durations of daytime dives and their lower frequency relative to night-time dives (Fig. 6).

Discussion

The dive data obtained from four pregnant Patagonian southern elephant seals suggest three conclusions: (1) the Patagonian seals do not feed primarily on the continental shelf; (2) they forage pelagically in temperate waters of the South Atlantic Ocean east of the rookery, not in more southerly waters as female elephant seals from some other colonies do; and (3) the general diving pattern of Patagonian females resembles that of seals from other colonies. We discuss these points.

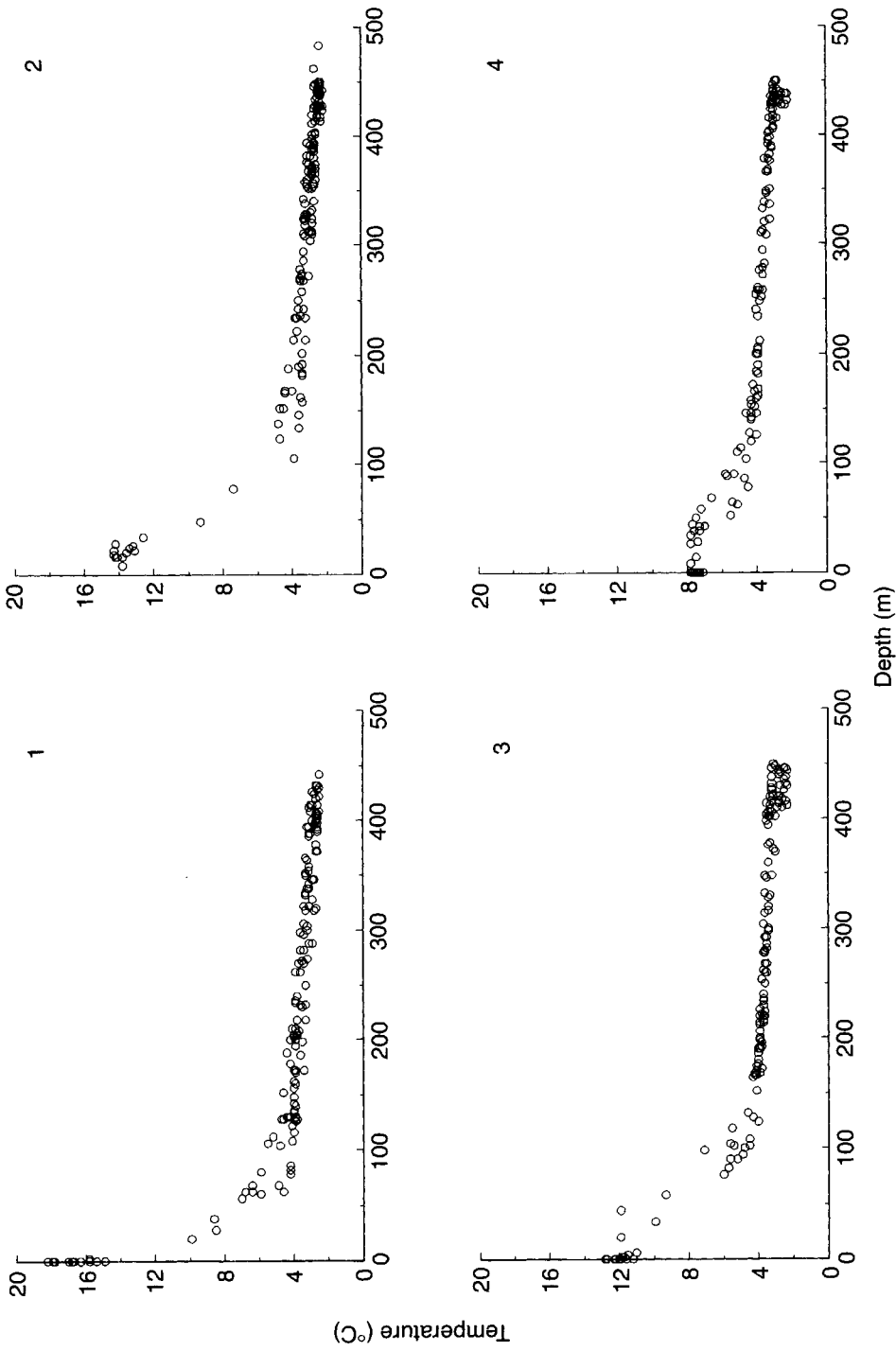


FIG. 4. Water temperature/depth profiles for each of four adult females from Patagonia during a day midway in the foraging period at sea.

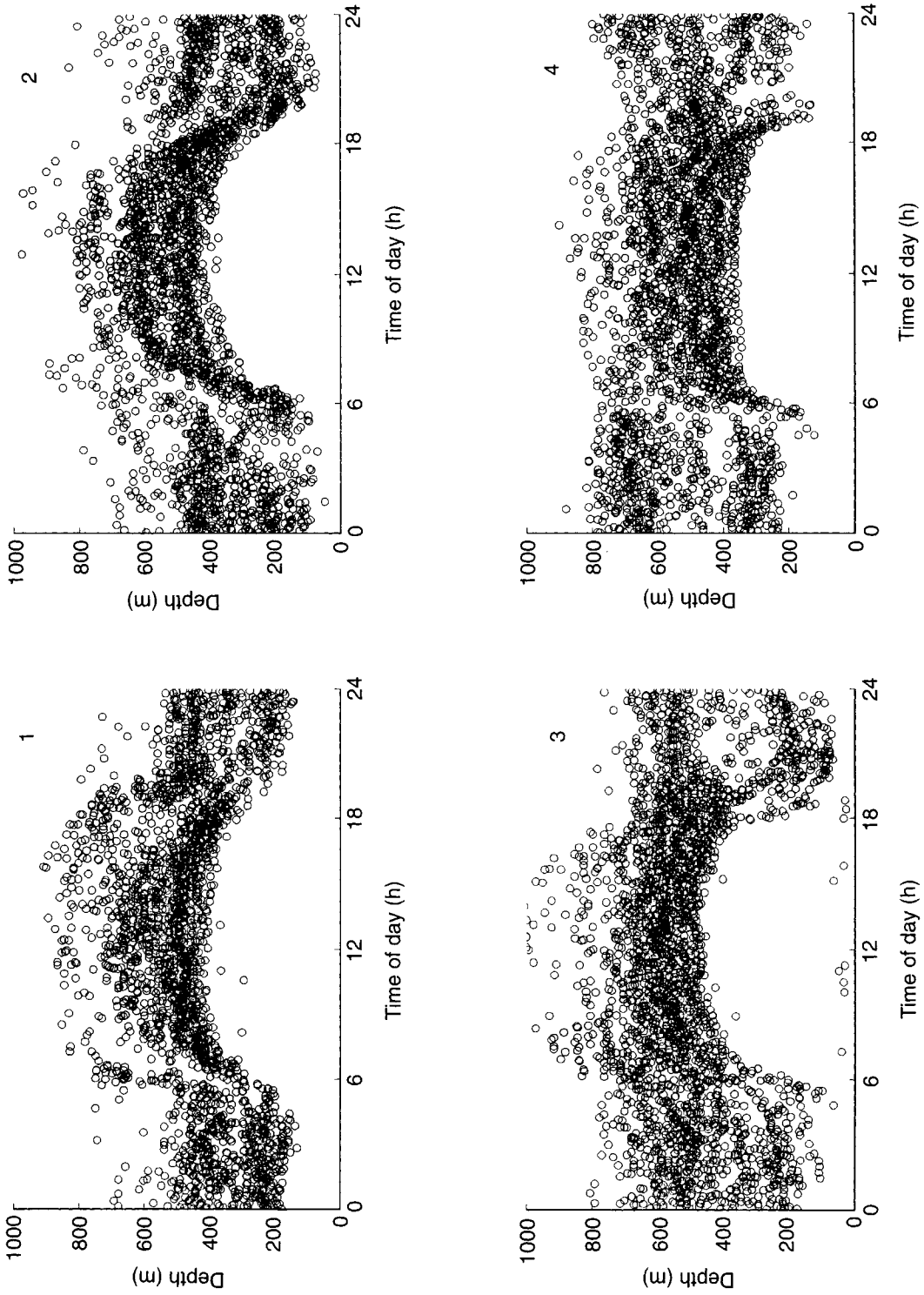


FIG. 5. Frequency distributions of the depth of D-type dives by time of day for four adult females from Patagonia.

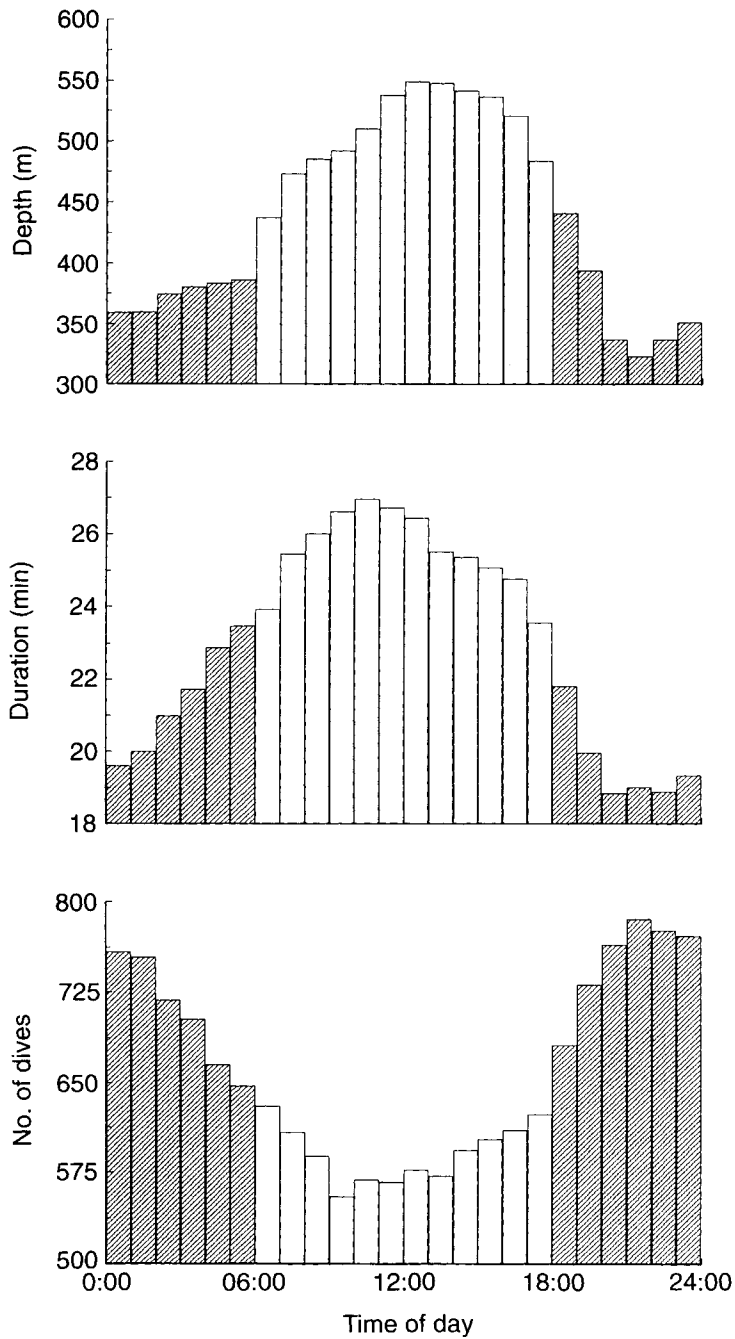


FIG. 6. Composite frequency distributions of all dives of four females from Patagonia showing dive depth, dive duration and number of dives as a function of time of day.

Absence of foraging on the continental shelf

It is clear from the speed at which females crossed the continental shelf when departing the rookery that little, if any, foraging occurred *en route* to deep water. The minimum mean horizontal swim speed of 1.61 ± 0.09 m/sec suggests rapid non-stop transit. The average daily velocity of three post-breeding females in the first transit phase of migration from South Georgia averaged approximately 1.0 m/sec (McConnell, Chambers & Fedak, 1992). The horizontal transit speed of a northern elephant seal bearing a swim speed recorder was 1.45 ± 1.87 m/sec on the continental shelf compared to 1.02 ± 1.93 m/sec off the shelf (Le Boeuf *et al.*, 1992). Consistent with rapid transit from the rookery to deep water, is the higher dive rate and decreased dive durations on the continental shelf compared to off the shelf. The shorter dive durations while crossing the shelf suggest higher oxygen utilization rates due to higher swim speeds (Le Boeuf & Crocker, 1995).

It is not clear why our sample of Patagonian elephant seals did not exploit prey on the shelf near the rookery. Southern elephant seals eat 15 or more species of cephalopods, most of which are a variety of squid (Rodhouse *et al.*, 1992). There are major fisheries for short fin squid, *Illex argentinus*, and common squid, *Loligo gahi*, on the Patagonian shelf south to the Falkland Islands (Csirke, 1987; Beddington *et al.*, 1990). *Illex* breeds on the shelf in late August and September (Brunetti & Ivanovic, 1992); mid water abundance of juveniles at this time is great on the shelf and negligible in the deep water where the seals in this sample spent their time. Argentine hake, *Merluccius hubbsi*, are abundant along the outer shelf and continental slope from May to August (Podestá, 1990); hake are a common prey item of northern elephant seals (Antonelis *et al.*, 1994). Two explanations come to mind for why the seals in our sample did not feed on the shelf. One is that the prey listed above are not eaten by southern elephant seals, they are not available, or other prey are more desirable. Studies of diet composition of Patagonian seals are required to confirm this. The other is that the seals eschew the prey on the shelf, minimizing time there, to reduce the probability of encountering their major predator, *Orcinus orca* (Lopez & Lopez, 1985; Hoelzel, 1991). Rapid shelf crossings and diving behaviour of northern elephant seals are consistent with the hypothesis that they reduce time in the danger zone where they are exposed to predation by white sharks, *Carcharodon carcharias* (Le Boeuf & Crocker, 1995).

Foraging location

The females in this sample foraged widely in the temperate waters of the South Atlantic Ocean never venturing into colder southern waters with mean SSTs below 6.9°C or temperatures at 100–500 m below 2°C . That is, they did not forage near, in, or south of the Antarctic Polar Front (APF), a temperature boundary where cold Antarctic surface water sinks below the warmer sub-Antarctic surface water with SST in the range $0\text{--}4^\circ\text{C}$. This is in marked contrast to female elephant seals studied from other colonies, most of whom foraged south of the APF below 50°S . Females from Macquarie Island either foraged around the APF or they utilized Antarctic waters south of 62°S , up to 1000 km south of the rookery (Hindell, Burton & Slip, 1991). Post-moult or pregnant females were similar in their migratory habits to non-pregnant females (Slip, Hindell & Burton, 1994). Three females from South Georgia migrated south-west up to 2650 km south to cold waters on the broad Antarctic continental shelf (Boyd & Arnborn, 1991; McConnell *et al.*, 1992; Fedak *et al.*, 1994). Three females from Marion Island migrated between 1,100–1,400 km from the colony and gave variable responses: one foraged south of

the APF where mean SSTs declined to -1.7° , one foraged near the sub-Antarctic front (SST = $5.3-7.3^{\circ}$) and one foraged near the subtropical convergence where mean SST reached 14.1° (Bester & Pansegrouw, 1992).

These results suggest that the Patagonian and, perhaps, some of the Marion Island seals, are foraging in quite different locations compared with seals from Macquarie and South Georgia. Seals from the latter colonies are migrating further than the Patagonian seals, in some cases, and into colder waters. McConnell *et al.* (1992) and Fedak *et al.* (1994) hypothesize that distant foraging is efficient when the destination, such as the Antarctic continental shelf, ice edges and Antarctic Polar Front are highly productive and the benefits of foraging outweigh the costs of travel. That is, a long swim on an empty stomach may, in the long term, be more productive than pelagic meandering in the open reaches of the ocean where prey are widely distributed temporally and spatially and are therefore, unpredictable. The South Georgia seals travelled directly up to 2650 km to reach their destinations. In contrast, the Patagonian seals meandered back and forth in the open ocean with one of them reaching a maximum distance of 1800 km from the rookery in 63 days. If the majority of seals from Patagonia use the same open ocean foraging strategy, it is evidently a productive one since the colony has been increasing in number during the last few decades. This issue deserves further study since geographic differences in foraging location may be associated, to variable degrees, with competition for resources, different responses to seasonally enhanced biological productivity, and differential effects of oceanographic variables on biological productivity, all mechanisms that may limit and regulate the population dynamics of each colony.

The diving pattern of Patagonian elephant seals compared to seals from other colonies

The overall diving-foraging pattern of pregnant Patagonian seals is similar to that of seals from other colonies such as South Georgia (Boyd & Arnborn, 1991), or Macquarie Island (Hindell, Slip & Burton, 1991; Slip *et al.*, 1994). There are no significant differences in mean dive depth, mean dive duration, mean surface intervals, or percentage time diving. The majority of dive types displayed by seals from Patagonia and from Macquarie Island (Hindell, Slip & Burton, 1991) were indicative of pelagic foraging in the deep scattering layer, with dives being deeper during the day than at night. This is consistent with feeding on animals such as squid in the water column. The general strategy of females appears to be to move continuously in search of a spatially distributed food source whose vertical distribution varies with time of day (Le Boeuf *et al.*, 1993).

We conclude that the major difference between the Patagonian seals and seals from other rookeries, whose numbers are either stable or in decline, is in the location of foraging.

We are indebted to Dr W. Conway and the New York Zoological Society for encouraging and supporting biological research in Patagonia. We thank Dr Mirtha Lewis, G. Aguilar, R. Baldi, C. Bisioli, L. I. Campagna and P. Nepomnanschy for their assistance in the field; Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut for permits to work in Península Valdés; and E. Prado, Centro Nacional Patagónico and Fundación Patagonia Natural for logistical support. Funded by grants from the National Geographic Society, the New York Zoological Society, Wildlife Conservation Society, the National Science Foundation, and a gift from the E. Macgowan Estate through the courtesy of Mr George Malloch.

REFERENCES

- Antonelis, G. A., Lowry, M. S., Fiscus, C. H., Stewart, B. S. & DeLong, R. L. (1994). Diet of the northern elephant seal. In *Elephant seals: Population ecology, behavior and physiology*: 211–223. Le Boeuf, B. J. & Laws, R. M. (Eds). Berkeley: University of California Press.
- Beddington, J. R., Rosenberg, A. A., Crombie, J. A. & Kirkwood, G. P. (1990). Stock assessment and the provision of management advice for the short fin squid fishery in Falkland Islands waters. *Fish. Res.* **8**: 351–365.
- Bellisio, N. B., López, R. B. & Torno, A. (1979). *Peces marinos patagónicos*. Secretaría de Estado de Intereses Marítimos. Subsecretaría de Pesca. República Argentina.
- Bestler, M. N. & Pansegrouw, H. M. (1992). Ranging behaviour of southern elephant seal cows from Marion Island. *S. Afr. J. Sci.* **88**: 574–575.
- Boyd, I. L. & Arnboim, T. (1991). Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biol.* **11**: 259–266.
- Briggs, G. D., Hendrickson, R. V. & Le Boeuf, B. J. (1975). Ketamine immobilization of northern elephant seals. *J. Am. vet. med. Ass.* **167**: 546–548.
- Brunetti, N. E. & Ivanovic, M. L. (1992). Distribution and abundance of early life stages in squid (*Illex argentinus*) in the south-west Atlantic. *ICES J. mar. Sci.* **49**: 175–183.
- Burton, H. (1986). A substantial decline in numbers of the southern elephant seal at Heard Island. *Tasm. Nat.* **86**: 4–8.
- Campagna, C. & Lewis, M. (1992). Distribution and growth of an elephant seal colony. *Mar. Mamm. Sci.* **8**: 387–396.
- Campagna, C., Lewis, M. & Baldi, R. (1993). Breeding biology of southern elephant seals in Patagonia. *Mar. Mamm. Sci.* **9**: 58–87.
- Clarke, M. R. & MacLeod, N. (1982). Cephalopods in the diet of elephant seals at Signy Island, South Orkney Islands. *Bull. Br. Antarct. Surv.* **57**: 27–31.
- Csirke, J. (1987). The Patagonian fishery resources and the offshore fisheries in the South-West Atlantic. *FAO Fish. Tech. Pap.* **286**: 1–75.
- DeLong, R. L., Stewart, B. S. & Hill, R. D. (1992). Documenting migrations of northern elephant seals using day length. *Mar. Mamm. Sci.* **8**: 155–159.
- Fedak, M. A., Arnboim, T., McConnell, B. J., Chambers, C., Boyd, I. A., Harwood, J. & McCann, S. (1994). Expenditure, investment and acquisition of energy in southern elephant seals. In *Elephant seals: Population ecology, behavior and physiology*: 354–373. Le Boeuf, B. J. & Laws, R. M. (Eds). Berkeley: University of California Press.
- Gordon, A. L. & Molinelli, E. J. (1992). *Southern Ocean atlas*. Surrey: Columbia University Press.
- Hill, R. D. (1994). The theory of geolocation by light-levels. In *Elephant seals: Population ecology, behavior and physiology*: 227–236. Le Boeuf, B. J. & Laws, R. M. (Eds). Berkeley: University of California Press.
- Hindell, M. A. (1990). *Population dynamics and diving behavior of southern elephant seals*. PhD thesis, Queensland University, Australia.
- Hindell, M. A. (1991). Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *J. Anim. Ecol.* **60**: 119–134.
- Hindell, M. A. & Burton, H. R. (1987). Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *J. Zool., Lond.* **213**: 365–380.
- Hindell, M. A., Burton, H. R. & Slip, D. J. (1991). Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. *Aust. J. mar. freshwat. Res.* **42**: 115–128.
- Hindell, M. A., Slip, D. J. & Burton, H. R. (1991). The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Aust. J. Zool.* **39**: 595–619.
- Hindell, M. A., Slip, D. J. & Burton, H. R. (1994). Possible causes of the decline of southern elephant seal populations in the Southern Pacific and Southern Indian Ocean. In *Elephant seals: Population ecology, behavior and physiology*: 66–84. Le Boeuf, B. J. & Laws, R. M. (Eds). Berkeley: University of California Press.
- Hoelzel, A. R. (1991). Killer whale predation on marine mammals at Punta Norte, Argentina: food sharing, provisioning and foraging strategy. *Behav. Ecol. Sociobiol.* **29**: 197–204.
- Laws, R. M. (1956). The elephant seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. *Sci. Rep. Falkl Isl. Depend. Surv.* No. 13: 1–88.
- Laws, R. M. (1960). The southern elephant seal (*Mirounga leonina* Linn.) at South Georgia. *Norsk Hvalfangsttid.* **49** (10): 466–76; (11): 520–542.
- Laws, R. M. (1977). Seals and whales of the Southern Ocean. *Phil. Trans. R. Soc. (B)* **279**: 81–96.
- Laws, R. M. (1994). History and present status of southern elephant seal populations. In *Elephant seals: Population ecology, behavior and physiology*: 49–65. Le Boeuf, B. J. & Laws, R. M. (Eds). Berkeley: University of California Press.

- Le Boeuf, B. J. (1994). Variation in the diving pattern of northern elephant seals with age, mass, sex and reproductive condition. In *Elephant seals: Population ecology, behavior and physiology*: 237–252. Le Boeuf, B. J. & Laws, R. M. (Eds). Berkeley: University of California Press.
- Le Boeuf, B. J., Costa, D. P., Huntley, A. C. & Feldkamp, S. D. (1988). Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Can. J. Zool.* **66**: 446–458.
- Le Boeuf, B. J. & Crocker, D. E. (1995). Diving behavior of elephant seals: implications for predator avoidance. In *Proceedings of the Symposium on the Biology of the White Shark*. Klimley, A. P. & Ainley, D. G. (Eds). Berkeley: University of California Press.
- Le Boeuf, B. J., Crocker, D. E., Blackwell, S. B., Morris, P. A. & Thorson, P. H. (1993). Sex differences in diving and foraging behaviour of northern elephant seals. *Symp. zool. Soc. Lond.* No. 66: 149–178.
- Le Boeuf, B. J. & Laws, R. M. (1994). Elephant seals: an introduction to the genus. In *Elephant seals: Population ecology, behavior and physiology*: 1–28. Le Boeuf, B. J. & Laws, R. M. (Eds). Berkeley: University of California Press.
- Le Boeuf, B. J., Naito, Y., Asaga, T., Crocker, D. & Costa, D. P. (1992). Swim speed in a female northern elephant seal: metabolic and foraging implications. *Can. J. Zool.* **70**: 786–795.
- Le Boeuf, B. J., Naito, Y., Huntley, A. C. & Asaga, T. (1989). Prolonged, continuous, deep diving by northern elephant seals. *Can. J. Zool.* **67**: 2514–2519.
- Lopez, J. C. & Lopez, D. (1985). Killer whales (*Orcinus orca*) of Patagonia, and their behaviour of intentional stranding while hunting nearshore. *J. Mammal.* **66**: 181–183.
- McCann, T. S. (1985). Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. In *Studies of sea mammals in southern latitudes*: 1–17. Ling, J. K. & Bryden, M. M. (Eds). Adelaide, Australia: South Australian Museum.
- McConnell, B. J., Chambers, C. & Fedak, M. A. (1992). Foraging ecology of southern elephant seals in relation to the oceanography of the Southern Ocean. *Antarct. Sci.* **4**: 393–398.
- Naito, Y., Le Boeuf, B. J., Asaga, T. & Huntley, A. C. (1989). Long-term diving records of an adult female northern elephant seal. *Antarct. Rec.* **33**: 1–9.
- Podestá, G. P. (1990). Migratory pattern of Argentine Hake *Merluccius hubbsi* and oceanic processes in the southwestern Atlantic Ocean. *Fish. Bull.* **88**: 167–177.
- Rodhouse, P. G., Arnbohm, T. R., Fedak, M. A., Yeatman, J. & Murray, A. W. A. (1992). Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Can. J. Zool.* **70**: 1007–1015.
- SAS Institute, Inc. (1985). *SAS User's Guide: Statistics. Version 5 edition*. Cary: SAS Institute, Inc.
- Slip, D. J., Hindell, M. A. & Burton, H. R. (1994). Diving behavior of southern elephant seals from Macquarie Island: an overview. In *Elephant seals: Population ecology, behavior and physiology*: 253–270. Le Boeuf, B. J. & Laws, R. M. (Eds). Berkeley: University of California Press.
- Skinner, J. D. & van Aarde, R. J. (1983). Observations on the trend of the breeding population of southern elephant seals, *Mirounga leonina*, at Marion Island. *J. appl. Ecol.* **20**: 707–712.
- Stewart, B. S. & DeLong, R. L. (1994). Post-breeding foraging migrations of northern elephant seals. In *Elephant seals: Population ecology, behavior and physiology*: 290–311. Le Boeuf, B. J. & Laws, R. M. (Eds). Berkeley: University of California Press.
- Vergani, D. F., Lewis, M. N. & Stanganelli, Z. B. (1987). Observation on haul-out patterns and trends of the breeding populations of southern elephant seals at Peninsula Valdés (Patagonia) and Stranger Point (King George Island). *SC-CCAMLR-VI/BG/36*: 1–9. Hobart, Tasmania.